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With this issue, the journal begins as a quarterly. It is anticipated that the coverage will be roughly what it has been in recent years. Also, it is expected that the number of printed pages per volume will be aproximately 376, about the same as recent volumes. To carry the journal forward, the Council of the New England Botanical Club has named Professor Albion R. Hodgdon, Chairman of the Department of Botany, University of New Hampshire, as Editor-in-

Chief. Associate Editors are listed on the front cover.

It is a pleasure for me to turn over the reins of Rhodora to Professor Hodgdon and to wish him every success in this new undertaking.

Added to my own efforts in editing Rhodora during the past eleven years have been those of a number of Club members acting in the capacity of Associate Editors. To these men, I should like to express publicly my appreciation. — REED C. ROLLINS.

# CHROMOSOME NUMBERS OF DYSSODIA (COMPOSITAE-TAGETINAE) AND PHYLETIC INTERPRETATIONS

#### MARSHALL C. JOHNSTON AND B. L. TURNER<sup>1</sup>

The genera Dyssodia Cav., Nicolletia Gray, Leucactinia Gray, Chrysactinia Gray, Porophyllum Adans., Lescaillea Griseb., Pectis L., Tagetes L., and Adenopappus Benth. together constitute a natural group characterized by the possession of oil glands and aromatic oils, and by the arrangement of the principal phyllaries in two subequal series and often united into a cup. This group, whose naturalness has not been questioned, has on the one hand been given tribal status as the Tagetinae or Tageteae (Cassini, 1829, 1834; Rydberg, 1915) and at the other extreme has been submerged in the Heliantheae in the broader sense (Cronquist, 1955), but it has usually been included in the Helenieae<sup>2</sup> as the subtribe Tagetininae (Bentham, 1873; Hoffmann, 1894; etc.)

Of the genera included, Dyssodia in the very broad sense of Hoffmann (1894) and of this paper, is the most diverse

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<sup>2</sup>That the tribe Helenieae is artificial (polyphyletic) has been suggested so often it scarcely bears repetition (Bentham, 1873; Small, 1919; Leonhardt, 1949; Cronquist. 1955; etc.). For suggestions as to the true affinities of certain included genera see Cronquist (1955), Turner (1956), Rock (1957), Turner and Johnston (1961), Turner, Ellison and King (1961), and Raven and Kyhos (1961) and papers cited by them.

from the standpoint of both morphology and cytology. Among its species, we find some plants which show combinations of the most specialized traits, and others which show combinations of the least specialized traits of the entire group. The ancestry of the other genera might well have comprised plants which would be placed in the genus *Dyssodia*, if they persisted today. *Dyssodia*, then, is of primary interest for an elucidation of phylogeny of the subtribe. The present paper tabulates the few chromosome counts for the genus already published along with the numerous original ones (Table 1). The counts are presented within the framework of a possible classification of the genus proposed by Rydberg (1915).

#### METHODS

Chromosome counts newly reported in the present paper were made from pollen mother cell squashes as outlined by Turner and Johnston (1961a). The microscopy was partly the work of Dr. W. L. Ellison and Mr. A. M. Powell, to whom we are much obliged. Camera lucida drawings were made at an initial magnification of ca. 2,000 diameters, and selected drawings are presented in Fig. 1-8. Voucher specimens (Table 1) are deposited in The University of Texas Herbarium. The determinations are our own.

#### OBSERVATIONS

Chromosome counts are reported for 45 populations of Dyssodia representing 17 species (Table 1). The gaps in our chromosomal knowledge are obvious. Most of these are due to the general unavailability of the taxa concerned. However, we may point out such a glaring omission as D. papposa which occurs from southern Ontario to southern Mexico, and is one of the most abundant roadside annuals in the high-lands of Mexico. The deficiencies stem from the difficulty encountered in attempting to get usable bud material in this genus as compared to the ease of obtaining usable material for some other Helenieae. Upwards of 250 bud-collections of Dyssodia have been received, from which are derived the 45 new counts presented here. The technical difficulties may partly be related to an abundance of oil in the buds which seems to interfere with proper fixation of the nuclear

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material, and partly to a propensity of the chromosomes to clump or fragment at meiosis. Perhaps a really thorough populational sampling, especially in the critical sections Thymophylla and Hymenatherum, may have to await the development of better techniques for working with meiotic chromosomes.

The section *Dyssodia*, containing the type species *D*. papposa, has a base of x = 13. These are plants of the Mexican highlands showing such unspecialized traits as retention of a calyculum and separate principal phyllaries. Our concept of *D. pinnata* includes *D. subintegerrima* Lag., and our concept of *D. papposa* (Johnston, 1956a) is likewise more inclusive than that of Rydberg (1915). Syncephalantha, a Central American segregate, is obviously part of *Dyssodia* from a morphological point of view and its chromosome base of x = 13 supports such a treatment.

The section Clomenocoma is primarily southern Mexican and Central American, with at least two Peruvian species. The only counts reported are from two species which are

anomalous in their ecogeography in that they occur in the Sonoran Desert. The base number, x = 13, is what one would expect when the relatively unspecialized character of the taxon is considered. It is probably that the whole section is on a base of x = 13.

Dyssodia porophylla and D. cancellata, both placed in the genus Lebetina by Rydberg, are morphologically very close to Dyssodia and also show a base of x = 13. They are wide-spread annual weeds in Mexico.

For Dyssodia acerosa of the section Aciphyllaea we have conflicting reports, one from the southwestern United States of n = 12 (Raven, *et al.*, 1961), four of our own tentative counts of n = ca. 13, and one clear, unequivocal count of n = 8. This is a widespread desert species of southwestern

United States and far south into Mexico that is fairly uniform morphologically. It may also be added that in an otherwise very difficult genus, this is one of the species we have found most difficult to work with cytologically, and that these preliminary data only serve to whet our curiosity.

Plants of the sections Gymnolaena and Adenophyllum of southern Mexico show combinations of some of the least specialized habits and involucres to be found in *Dyssodia*. It is perhaps from among these sections that we may find species most closely resembling the ancestral types for the entire genus. Unfortunately, we have no chromosomal information for either of these sections.

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Dyssodia tagetoides, endemic to Texas and Oklahoma (Johnston, 1956a), and placed in the monotypic genus Dysodiopsis by Rydberg, remains unknown cytologically in spite of several attempts to obtain counts.

The section Thymophylla comprises several species of low perennial herbs and shrublets of the dry areas of Mexico, Arizona, New Mexico and western Texas, showing certain specializations such as fusion of the principal phyllaries into a cup and suppression of the calyculum. The section is of special interest for several reasons, not the least of these being that in the vicariad Dyssodia Belenidium -D. Thurberi it shows the bicentric geography, northern Argentina - northern Mexico, which parallels the geographic distributions of so many other plants (I. M. Johnston, 1940; Garcia, Soto, and Miranda, 1961; etc.) and which may indicate an antiquity of perhaps tens of millions of years (Croizat, 1952). Although D. Thurberi is morphically identical to D. Belenidium (Johnston, 1956a and 1956b), we here list the names separately because of the report that 2n = 32 in D. Belenidium, whereas we have found that n = 13 in the single population of D. Thurberi from which we have been able to obtain countable chromosomes. The further discovery of the number n = 13 in three other species of this section leads to a suspicion that the report for D. Belenidium may be in error and at least needs confirmation.

Dyssodia pentachaeta, in the inclusive sense (Johnston,

1956a), is rather polymorphic and might be broken into several species satisfactorily. Extensive population sampling for cytological data is desirable, but the six counts here reported do not offer much hope that chromosome numbers *per se* will be helpful in an elucidation of the taxonomy. Moreover, we have found *D. pentachaeta* one of the most

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difficult species from which to obtain countable material. The preliminary indication of two levels of ploidy in the somewhat polymorphic taxon D. setifolia (sensu Johnston, 1956a) also indicates that further sampling is desirable. The section Hymenatherum is closely related to section Thymophylla. Even so ardent a proponent of segregate genera as Rydberg (1915) placed them together, in the genus Thymophylla. The species of section Hymenatherum show a greater specialization than those of any others of the genus. They are all annuals of the Texano-Mexican dry areas, some of them being much reduced ephemeral desert annuals. The calyculum is entirely suppressed and the involucral fusion proceeds so far that in several species the individual phyllaries are scarcely discernible. Furthermore the base chromosome number x = 8 prevails among these plants. These facts, together with the additional character that most of the section Thymophylla have strictly opposite leaves and branches whereas Hymenatherum shows an alternate arrangement, at least in the upper parts of the stems, might lead to the resurrection of Hymenatherum to the generic level. But other evidence militates against such a move, viz. the evidence presented here that in Dyssodia tenuiloba the group is dibasic with one population clearly showing n = 13, another n = 8, and observations by the senior author of a group of plants which were probably the result of hybridization between D. tenuiloba and D. pentachaeta, at one locality just south of Monterrey, Nuevo León (unfortunately, the station has now been obliterated by enlargement of a gravel pit). Dyssodia micropoides, a species of depressed annuals with a clearly defined distribution largely restricted to the dry limestone piedmont of Coahuila and Nuevo León (Johnston, 1956a), has been something of an orphan, with no clear line of descent within the genus. Rydberg (1915) placed it, as the genus Gnaphaliopsis, immediately following his genus Thymophylla. The discovery of n = 8 for this taxon suggests that the species might best be placed near or with the section Hymenatherum.

The rare species, Dyssodia neomexicana, deserves special

comment for several reasons, one being that the present report extends the known distribution several hundred miles to the south. The species has previously been reported from Chihuahua, from the type locality in southwestern New Mexico, and from Apache County, Arizona. The plants are ephemeral annuals with opposite leaves below, alternate above, and an involucre very much like that of *D. aurea* of the section Hymenatherum except for larger size and the constant presence of a calyculum of a few linear bractlets.

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FIG. 1-8. — Camera lucida drawings of the meiotic chromosomes of Dyssodia spp. — Fig. 1. D. micropoides (n = 8). — Fig. 2. D. neomexicana (n = 7). — Fig. 3. D. Treculii (n = 16). — Fig. 4. D. tenuifolia (n = 8). — Fig. 5. D. acerosa (n = 8). — Fig. 6. D. aurea (n = 8). Fig. 7. D. tagetiflora (n = 13). — Fig. 8. D. decipiens (n = 13). (X ca. 2000).

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Rydberg (1915) placed the species in his monotypic genus *Trichaetolepis*, next to his segregate genus *Dysodiopsis*. We list the species among Hymenatherum largely because of lack of any other place to put it and because of the discovery of the low number of n = 7, which stands alone in the genus. DISCUSSION

The "gap" between x = 8 and x = 12, 13 in this genus has

been mentioned by Turner, et al. (1961) and compared to gaps in such genera as Aster, Chrysopsis, Gutierrezia and Inula. The idea that the present gap in Dyssodia is the result of inadequate sampling must not be rejected summarily. But dismissing it momentarily, we might suggest another explanation. The gaps, at least in some genera, not including Dyssodia, have been explained as the result of an uploid loss to fairly low numbers (ca. 5) from an ancestral base of x = ca. 9 (this hypothesis, or a modification of it, has been presented by several authors, Stebbins, et al., 1953; Huziwara, 1958; Raven, et al., 1960, etc.). On the other hand, Turner, et al. (1961) think it more plausible to postulate a fairly low ancestral base for the family (x = 4 or 5) and to consider the probability that in various phyletic lines we may detect aneuploid loss or gain in series both from the ancestral base and from derivative multiples of it. At any rate, regardless of the true etiology, we would like to reiterate the absence of any known mechanism to explain differential survivorship (i.e., natural selection) of certain chromosome numbers as compared to other chromosome numbers in the same phyletic or in the same aneuploid series. Nor does it appear likely that such a mechanism will suddenly come to light as a deus ex machina for the aneuploid-reduction loss hypothesis, or as an explanation of the situation in Dyssodia.

The gap in the Dyssodia series which includes numbers of

n = 9, 10, 11, is not strictly comparable to the gap of x = 6, 7 and/or 8 in the genera named above. In the latter genera the counts clustering at 9 and 10 are very nearly double those clustering at 4 and 5, whereas in *Dyssodia* the higher bases of x = 12, 13 are not double the common lower base of x = 8. If we postulate an ancestral base x = 8 we must ex-

plain away a new "gap" of x = 14, 15, and if we postulate an ancestral base of x = 7, we must explain the present rarity of n = 7 and n = 14. Furthermore, in Dyssodia the gap occurs not simply between species or species groups but even within groups of plants so similar morphically that they have been considered to constitute a single species (e.g., D.

Belenidium, D. tenuiloba, and D. acerosa). If one assumes an ancestral basic chromosome number of x = 4 for the genus Dyssodia, then much of the difficulty in explaining the



#### Section or species group:

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LEBETINA	x · 13
SYNCEPHALANTHA	x · 13
DYSSODIA	x · 13
ADENOPHYLLUM	x · ?
CLOMENOCOMA	x · 13
D. acerosa	x · 8, 12, 13
THYMOPHYLLA	x . 8(?),13
HYMENANTHERUM	x · 8.13



# TAGETINEAN ANCESTOR

FIG. 9. Hypothetical phyletic relationships among genera, sections, and species of the genus Dyssodia and related genera.

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#### TABLE 1. SPECIES OF DYSSODIA ARRANGED IN A TENTATIVE CLASSIFICATION TOGETHER WITH AVAILABLE CHROMOSOME COUNTS

	Voucher specimens	Chromosome Nos.	
Taxa	and/or literature reference	n	2n

Sect. Dyssodia D. papposa (Vent.) Hitchc.<sup>c</sup> D. tagetiflora Lag.

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10

#### D. pinnata (Cav.) Rob.



QUERÉTARO: 8 mi. n. of Querétaro, Johnston 4026A. 13 (Fig. 7) OAXACA: Oaxaca, King 2942. 13 VERA CRUZ: 10 mi. sw. of No-13gales, King 2337. SAN LUIS POTOSI: La Capilla, 13Rock M-452. TAMAULIPAS: 11 mi. s. of Palmil-13las, Johnston 5623. MEXICO: 10 mi. w. of Toluca, 13King 3591. MEXICO: Rte. 55, 3 mi. from junction with Rte. 57, Powell 13& Edmondson 582. MEXICO: Rte. 57, 29 mi. s. of tollgate, Powell & Edmondson 584. 13

Sect.<sup>a</sup> [Genus Syncephalantha Bartl.] D. decipiens (Bartl.) M. C. Johnston<sup>b</sup> " " Sect. Clomenocoma (Cass.) O. Hoffm. D. grandiflora DC.<sup>c</sup>

 OAXACA: 10 mi. n. of Oaxaca,
 13

 King 2490.
 13

 OAXACA: 3 mi. se. of Oaxaca,
 13

 King 3468.
 13

 OAXACA: 9 mi. nw. of Oaxaca,
 13

 King 3514.
 13

 CHIAPAS: 19 mi. ne. of Las
 13 (Fig. 8)

D. remota Blake<sup>c</sup> D. montana (Benth.) Gray<sup>c</sup> D. squarrosa Gray<sup>c</sup> D. speciosa Gray<sup>c</sup> D. aurantia (L.) Rob.<sup>c</sup> D. Cooperi Gray D. porophylloides Gray Sect.<sup>a</sup> [Genus Lebetina Cass.]

D. Jelskii Hieron.<sup>e</sup>

Raven and Kyhos (1961) Raven and Kyhos (1961)

13

26

	Voucher specimens	Chromosome Nos.	
Taxa	and/or literature reference	n	2n

D. cancellata (Cass.) Gray

AGUASCALIENTES: 4 mi. s. of Aguascalientes, Rock M-465. 13 DURANGO: 47 mi. n. of Durango. Powell & Edmondson 956. ca. 13

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D. porophylla (Cav.) Cav.

Sect. Gymnolaena DC.<sup>c</sup> D. oaxacana Greenm. D. serratifolia DC. D. integrifolia Gray D. Seleri Rob. & Greenm. Sect. Adenophyllum (Pers.) O. Hoffm.<sup>c</sup> D. coccinea Lag. Sect. Aciphyllaea DC. D. acerosa DC.

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TAMAULIPAS:5-6mi.nw.ofOcampo, King 3957.13GUANAJUATO:18mi.w.ofSala-13

Raven and Kyhos (1961) 24TEXAS: Crockett Co., 25 mi. w. of Ozona. Johnston 6407. 13TEXAS: Val Verde Co., Del Rio, Johnston 6489. 13**TEXAS:** Brewster Co., Elephant Mesa, Johnston 6423.  $13^{d}$ TEXAS: Brewster Co., 14 mi. e. of Marathon, Johnston 6454. 8 (Fig. 5) COAHUILA: 5 mi. w. of Saltillo. Powell & Edmondson 517. 13<sup>d</sup>

Sect.<sup>a</sup> [Genus Dysodiopsis (A. Gray) Rydb.]<sup>c</sup> D. tagetoides T. & G. Sect. Boeberastrum Gray<sup>c</sup> D. littoralis Brandg. D. anthemidifolia Benth. D. concinna (A. Gr.) Rob. Sect.<sup>a</sup> [Genus Urbinella Greenm.]<sup>c</sup> D. Palmeri (Greenm.) Macbr. D. Gentryi M. C. Johnston Sect. Thymophylla (Lag.) O. Hoffm. D. tephroleuca Blake<sup>c</sup> D. setifolia (Lag.) Rob. var. setifolia 4186.

COAHUILA: Carneros, Johnston 26

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# 12Rhodora[Vol. 64Voucher specimensTaxaVoucher specimensChromosome Nos.and/or literature referencen2n

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D. setifolia (Lag.) Rob. var. setifolia " SAN LUIS POTOSI: 8 mi. w. of Rioverde, Johnston 5649. TAMAULIPAS: 11 mi. s. of Palmillas, Johnston 5629. ca. 26 NUEVO LEÓN: 41 m. s. of Saltillo, Rock M-274. ca. 26

26

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D. setifolia var. Greggii (Gray)
M. C. Johnston<sup>c</sup>
D. aurantiaca (Brandg.) Rob.<sup>c</sup>
D. Belenidium (DC.) Macl.
D. Thurberi (Gray) A. Nels.

D. Hartwegii (Gray) Rob.

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D. pentachaeta (DC.) Rob. sensu lato

Covas and Schnack (1946) TEXAS: Brewster Co., 1 mi. n. of Black Gap, Johnston 6443. 13 SAN LUIS POTOSI: 11 mi. e. of San Luis Potosí, Johnston 4040a. 26DURANGO: 57 mi. ne. of Durango, King 3761. ca. 26 NUEVO LEÓN: 30 m. s. of Saltillo, Ellison 51. 13COAHUILA: 5 mi. w. of Allende, Johnston 4169. 13COAHUILA: 5 mi. w. of Saltillo, Powell & Edmondson 516. ca. 13 SAN LUIS POTOSI: 8 mi. w. of Rioverde, Johnston 5648.  $13^{d}$ TEXAS: Brewster Co., 8 mi. w. of  $13^{d}$ Marathon, Johnston 6449. TEXAS: Pecos Co., southern tip of co., Johnston 6457. ca. 13 TEXAS: Kinney Co., 8 mi. e. of  $13^{d}$ Brackettville, Johnston 6490.

D. pentachaeta (DC.) Rob.
sensu lato
D. pentachaeta (DC.) Rob.

sensu lato

D. pentachaeta (DC.) Rob.

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Sect. Hymenatherum (Cass.) O. Hoffm. D. tenuiloba (DC.) Rob.

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TEXAS: Webb Co., Laredo, Johnston 5466. TEXAS: Brooks Co., 3 mi. e. of

#### D. Wrightii (Gray) Rob.

Falfurrias, Johnston 5467.8°TEXAS: San Patricio Co., 3 mi. n.of Sinton, Johnston 5468.8TEXAS: Goliad Co., 1 mi. w. ofRefugio Co. line, Johnston 5471.Refugio Co., 2 mi. n. ofAransas River, Johnston 5469.ca. 8

	Voucher specimens	Chromoson	ne Nos.
Taxa	and/or literature reference	n	2n
D. Treculii (Gray) Rob.	TEXAS: Val Verde Co.,	Del Rio,	
D. Lawrence Comme	Johnston 6488.	16	(Fig. 3)
D. texana Cory			
D. mutica M. C. Johnston	Johnston (1960)	8	

D. aurea (Gray) A. Nels. var.

aurea

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D. aurea var. polychaeta (Gray) M. C. Johnston

D. anomala (Canby & Rose) Rob.<sup>c</sup>

D. tenuifolia (Cass.) Loes.
(Incl. D. Neaei (DC.) Rob.
and D. diffusa (Gray) Rob.)
D. neomexicana (Gray) Rob.

COAHUILA: Bolsón de Mapimí, Rock M-484. 8 COAHUILA: 10 mi. e. of San Pedro de las Colonias. Powell & Edmondson 520. 8<sup>d</sup> CHIHUAHUA: 14 mi. n. of Parral, Powell & Edmondson 972. 8 CHIHUAHUA: just east of Chihuahua City, Powell & Edmondson 1018. 8 (Fig. 6)

SAN LUIS POTOSI: 7 mi. e. of San Luis Potosí, Johnston 4041.

8 (Fig. 4) 8

Sect.<sup>a</sup> [Genus Gnaphaliopsis DC.] D. micropoides (DC.) Loes.

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Same locality, Johnston 5638. 8 MEXICO: 36 mi. s. of tollgate north of Mexico City, Powell & Edmondson 588. 7<sup>e</sup>(Fig. 2)

NUEVO LEON: w. of Monterrey,<br/>Rock M-496.8NUEVO LEON: 26 mi. s. of Sa-<br/>binas Hidalgo, Johnston 5455.8COAHUILA: San Lázaro, John-<br/>ston 4184.8 (Fig. 1)

<sup>a</sup>No nomenclatural combination has been published for this taxon at the proper rank. Formal changes in status are not deemed appropriate for this contribution, but must await a formal taxonomic treatment.

<sup>b</sup>Dyssodia decipiens (Bartl.) M. C. Johnston, comb. nov., based on Syncephalantha decipiens Bartl., Ind. Sem. Hort. Goett. 1836: 6. 1836.

<sup>c</sup>No chromosome counts have been made or reported for this taxon. <sup>d</sup>One or two fragments were also seen. eThis count was quite clear and unequivocal.

obvious gap is removed. Thus taxa with n = 8 would be tetraploid; n = 12, hexaploid; and taxa with n = 7 and 13 aneuploid derivatives from such taxa. The fact that at least

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one species, *D. acerosa*, has chromosome numbers n = 8, 12, 13 might be explained by the hypothesis of Turner, *et al.* (1961) that the Compositae showed a very rapid and explosive evolution while still at the predominately diploid level of x = 4 and 5, most of the generic lines being formed at that time. Surviving diploid taxa, in that they are for the most part not buffered against mutational change (Stebbins, 1950) and are thus more prone to rapid evolution, should be relatively more specialized. The data and some of our speculations are summarized in Fig. 9. We can do no more at present than to pose the problems and remark that at the very least the picture must tantalize the would-be phylogenist. — THE PLANT RESEARCH INSTITUTE, DEPARTMENT OF BOTANY, THE UNIVERSITY OF TEXAS, AUSTIN

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# THE PARASITIC BEHAVIOR OF MELAMPYRUM LINEARE AND A NOTE ON ITS SEED COLOR<sup>1</sup>

# MARTIN A. PIEHL

Parasitism has been described for several members of the genus *Melampyrum*, the cow-wheats (Scrophulariaceae), beginning with *M. arvense* of Europe (Decaisne, 1847). To my knowledge, however, a parasitic existence has not been substantiated for *M. lineare*, the single North American representative of the genus. Fraysse (1906) ascribes to Heinricher (1904) the assertion that all species of the genus are parasitic; however, the latter actually said (p. 412), "Alle untersuchen Arten der Gattung *Melampyrum* sind parasitisch (*M. arvense, barbatum, nemorosum, silvaticum, pratense*)", and no reference was made to *M. lineare*. Shreve

<sup>1</sup>Contribution from the University of Michigan Biological Station.